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## Come to the dark side! The role of functional traits in shaping dark diversity patterns of south-eastern European hoverflies

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1    **Come to the dark side! The role of functional traits in shaping**  
2    **dark diversity patterns of Southeast European hoverflies**

3

4    Short title: Hoverfly dark diversity in SE Europe

5

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21

22    **Abstract**

23 Dark diversity represents the set of species belonging to a species  
24 pool but is not locally present, i.e. species that are currently  
25 'missing' from a site but have the potential to occur there. The  
26 concept allows characterization of the mechanisms determining  
27 why species are sometimes absent from an area that seems  
28 ecologically suitable for them. Our aim was to assess the dark  
29 diversity of hoverflies (Diptera: Syrphidae) in Southeast Europe  
30 and to discuss the role of different functional traits that might  
31 increase the likelihood of species contributing to dark diversity.  
32 Based on expert opinion, the Syrph the Net database and known  
33 occurrences of species, we estimated observed, potential and dark  
34 diversities within each defined vegetation class for 564 hoverfly  
35 species registered in SE Europe. To detect the most important  
36 functional traits of species contributing to dark diversity across  
37 classes, we used a random forest algorithm and respective statistics  
38 for variable importance (%IncMSE). The highest dark diversity  
39 was found for Southwest Balkan sub-Mediterranean mixed oak  
40 forests, whereas the lowest was in Mediterranean mixed forests.  
41 Three larval feeding modes (saproxylic, and phytophagous of  
42 bulbs or roots) were found to be most important for determining  
43 the probability of a species contributing to hoverfly dark diversity,  
44 based on univariate correlations and random forest analysis. This  
45 study shows that studying dark diversity might provide important

46 insights into what drives community assembly in this taxon and  
47 region, especially its missing components and contributes to more  
48 precise conservation prioritization of both hoverfly species and  
49 their habitats.

50

51 **KEYWORDS:** disturbance; functional characteristics; insects;  
52 missing species; richness; Syrphidae; vegetation classes

53

## 54 **Introduction**

55 In order to understand and try to alleviate the negative  
56 consequences of biodiversity loss, detailed information on different  
57 aspects of biodiversity is essential (Hooper *et al.*, 2005; Barton &  
58 Evans, 2017). Data on extant biodiversity may not allow  
59 interesting patterns related to missing components of communities  
60 to be uncovered (Pärtel *et al.*, 2011). Recent findings (Pärtel, 2011,  
61 2014; Lewis *et al.*, 2017) have shown that so-called ‘dark  
62 diversity’ could reveal new biodiversity patterns that would not be  
63 evident from investigating only observed diversity (Ronk *et al.*,  
64 2015). In order to examine dark diversity of a target site, the  
65 habitat-specific species pool must be established, i.e. the set of  
66 species that can inhabit a given area under designated ecological  
67 conditions (Cornell & Harrison 2014; Zobel, 2016). The species  
68 that are not recorded at a particular site, but that belong to its

69 species pool and could potentially co-occur in the site given its  
70 biotic, abiotic processes and dispersal limitations, constitute the  
71 dark diversity of that site (Pärtel *et al.*, 2011). In other words, dark  
72 diversity represents the absent element of a habitat-specific species  
73 pool (Lewis *et al.*, 2017). Importantly, a species pool is not simply  
74 the sum of observed and missing species (Fig. 1). Although total  
75 observed diversity consists of species that belong to the habitat-  
76 specific species pool, it also comprises species that are currently  
77 present in a particular community but are not part of the pool.

78

79 Figure 1. Schematic diagram illustrating species pool, observed  
80 and dark diversity.

81

82 Hoverflies (Diptera: Syrphidae) play important roles in providing  
83 vital ecosystem services such as pollination (Ssymank & Kearns,  
84 2009; Petanidou *et al.*, 2011; Jauker *et al.*, 2012), waste  
85 decomposition (Gilbert, 1985) and biological control (White *et al.*,  
86 1995; Blaauw & Isaacs, 2012; Day *et al.*, 2015). Recent studies  
87 have shown that hoverflies can serve as valuable model organisms  
88 in terms of studies of climate change (Kalooveloni *et al.*, 2015;  
89 Radenković *et al.*, 2017; Miličić *et al.*, 2018), urbanization (Bates  
90 *et al.*, 2011; Verboven *et al.*, 2014), landscape structure (Power *et*

91 *al.*, 2016) or land use (Aguirre-Gutiérrez *et al.*, 2015, Földesi &  
92 Kovács-Hostyánszki, 2016; Lucas *et al.*, 2017).

93 Southeast Europe (SE Europe) is one of the richest areas globally  
94 in terms of hoverfly diversity, mostly due to its complex geology  
95 (Cvetković *et al.*, 2015) and climatic diversity (Vukelić *et al.*,  
96 2018). Pronounced human-induced environmental changes have  
97 taken place in this region and left their mark on its vegetation.  
98 Considering the close connection of hoverflies to their habitats,  
99 this environmentally heterogeneous region is particularly suitable  
100 for examining biological and ecological responses of hoverflies to  
101 contrasting habitat types.

102 Ecological studies of hoverflies increasingly use functional traits  
103 (i.e. physiological, phenological, morphological or behavioral  
104 characteristics), rather than simply focusing on their taxonomic  
105 identity. Various authors have examined the response of hoverfly  
106 functional diversity to different environmental aspects including  
107 land use and land management (Schweiger *et al.*, 2007, de Groot *et*  
108 *al.*, 2016, Winsa *et al.*, 2017), climate change (Aguirre-Gutiérrez *et*  
109 *al.*, 2016) or habitat heterogeneity (Larrieu *et al.*, 2015). However,  
110 which functional traits promote the absence of species from  
111 apparently suitable sites (missing species), hence promoting higher  
112 levels of hoverfly dark diversity, remains unanswered.

113 This study for the first time tests the hypothesis that functional  
114 traits affect dark diversity of hoverflies, revealing ecological  
115 patterns reflected in hoverfly communities. Based on known  
116 occurrence records of hoverflies in SE Europe, the Syrph the Net  
117 (StN) database (Speight *et al.*, 2015), and expert opinion, we aim  
118 to assess the dark diversity of hoverflies in this region, as well as  
119 discuss the role of different functional traits in explaining the  
120 patterns of dark diversity.

121

## 122 **Methods**

### 123 **Study area and species occurrences**

124 This study includes all available information on SE European  
125 hoverflies. In a geographical sense, this area covers the Balkan  
126 Peninsula and the Aegean islands governed by Greece. Based on  
127 field collecting in this region and extensive literature review, we  
128 compiled a list of hoverfly species occurring in SE Europe.

129 Information on the distribution of registered species was extracted  
130 from the database of the Faculty of Sciences, University of Novi  
131 Sad, Serbia (FSUNS). This database is a result of the hoverfly  
132 monitoring program across investigated area from 1950 to 2017,  
133 during which the sampling of hoverflies was conducted using a  
134 consistent census protocol (see Radenković *et al.*, 2017 for more  
135 details). Additionally, we included data from published material

referring to this territory, as well as data obtained from different museum and private collections. Only specimens for which precise distributional data were available were used in our analyses. Exact locality coordinates were checked for accuracy where provided. Records for which only locality names were available were assigned coordinates using Google Earth (Google Inc., 2018). In total, we considered 63814 occurrence records of 564 species.

#### **Vegetation types**

To assess the distribution of hoverflies within different vegetation types represented in SE Europe, we used the map of natural vegetation of Europe (Bohn *et al.*, 2000/2003). In order to correspond with known biological and ecological characteristics of hoverfly species, we merged certain vegetation classes to generate a total of 11 classes (Fig. 2).

Figure 2. Vegetation classes in Southeast Europe.

#### **Functional traits**

Data on functional traits of hoverflies were collected from multiple sources. We used published data (Speight *et al.*, 2015; Speight, 2017), expert opinion-based data, and fieldwork experience spanning 35 years regarding biological and ecological



159 characteristics of species. Information on wing length of analyzed  
160 species was not available in the literature, but because we  
161 considered this trait to be biologically significant, we measured it  
162 using a Nikon SMZ 745T stereomicroscope. We measured four  
163 specimens of each species (two male and two female), and used the  
164 averaged value as a variable in further analyses. Functional traits  
165 with multiple non-mutually-exclusive trait states were coded as  
166 dummy variables. Additionally, if possible and where justified,  
167 categorical traits were transformed into ordinal variables. If the  
168 trait state for the given species was unknown, the species was  
169 assigned the most common trait state found in other members of  
170 that genus. The list of functional traits used in the analyses is  
171 presented in Tab. 1.

172

173 Table 1. Functional traits and trait states of hoverflies in SE  
174 Europe.

175

#### 176 **Estimation of dark diversity**

177 Species pools for each defined vegetation type separately were  
178 compiled based on expert opinion and information from the StN  
179 database. Each species was assigned to any  
180 major vegetation type in SE Europe defined in this study in which  
181 it can occur, taking into consideration its known distribution across

182 Europe, as well as the known biological and ecological preferences  
183 of that species (Speight *et al.*, 2015; Speight, 2017).  
184 All estimations and statistics were made using the full dataset  
185 (across vegetation types). To quantify observed diversity,  
186 occurrence records were plotted on the vegetation map using open  
187 source GIS software (QGIS Development Team, 2009). Dark  
188 diversity was calculated for each vegetation type separately as the  
189 difference between the species pool and the observed species  
190 belonging to that particular pool (i.e. the number of potential  
191 species missing from each pool). Percentage of dark diversity  
192 across all vegetation classes was calculated as the ratio between  
193 dark diversity and the sum of dark and observed diversity.

194

### 195 **Statistical analyses**

196 Our goal was to verify if species with certain traits were more  
197 likely to contribute to dark diversity. Therefore, our response  
198 variable was the proportion of times each species belonged to dark  
199 diversity in relation to its potential diversity across vegetation  
200 classes, termed herein the ‘dark diversity index’ (DDi). The  
201 explanatory variables were functional traits (or trait states) of  
202 species.

203 In a first step, we checked for correlations among functional traits.  
204 Spearman’s rank correlations were conducted for continuous

205 variable comparisons, Mann-Whitney tests for continuous-  
206 categorical variable comparisons, and Eta correlation coefficients  
207 were generated for categorical variable comparisons. Values above  
208 0.7 were considered indicative of collinearity (Dormann et al.,  
209 2013).

210 Next, we assessed the univariate correlation between functional  
211 traits and dark diversity; for categorical/binary variables we used  
212 the Kruskal Wallis test, whereas Spearman rank correlation was  
213 used for continuous and ordinal variables.

214 Even if some traits were not revealed to be important in univariate  
215 correlations, they might be important only when other factors are  
216 also considered. To establish the unique contribution of each trait  
217 to the probability of being part of dark diversity, we used a random  
218 forest (RF) regression model (Breiman, 2001), implemented within  
219 the randomForest R package (Liaw & Wiener, 2002). In this  
220 analysis, the number of trees (ntree) was set to 5000, and the  
221 number of predictors sampled for splitting at each node (mtry) was  
222 set to 6, which represents the default value suggested for  
223 regression RF models, i.e. number of predictor variables/3. Node  
224 size (nodesize) was kept as default, i.e. 5 for regression. After  
225 running the model, and in order to verify if species with certain  
226 traits were more likely to contribute to dark diversity, we  
227 quantified the importance of each predictive variable by

calculating the Mean Decrease Accuracy (%IncMSE). Merrill (2009) demonstrated that this latter measure provides the highest stability compared to node purity measures.

## **Results**

### **Species pool, observed species and dark diversity**

The number of species representing observed and dark diversity, as well as species complements of the species pools, varied between different vegetation classes (Fig. 3).

Figure 3. Number of species in dark diversity, observed diversity and in the species for each vegetation class.

The mean number of species for species pools was 276.1 ( $\pm 39.1$  SD), for observed diversity it was 242.7 ( $\pm 66.3$  SD), and for dark diversity it was 83.0 ( $\pm 39.6$  SD) across all vegetation classes. The most diverse species pool (355 species) was in Beech and mixed beech forests (E), whereas Acidophilous oak and mixed oak - hornbeam forests (D) exhibited the most hoverfly-species-poor pool (227 species) (Fig. 3). In terms of numbers of observed species, the richest vegetation class (402 species) was again beech and mixed beech forests (E), and the lowest number of observed hoverfly species (136 species) was recorded from Southwest

251 Balkan sub-Mediterranean mixed oak forests (H). Hoverfly dark  
252 diversity was lowest in Mediterranean mixed forests (J) (33  
253 species, 11.9%) and in Beech and mixed beech forests (E) (36  
254 species, 10.1%), and highest in Southwest Balkan sub-  
255 Mediterranean mixed oak forests (H) (162 species, 62.8%) and in  
256 Alpine, subalpine and oro-Mediterranean vegetation (A) (140  
257 species, 45%).

258

### 259 **Dark diversity and functional traits**

260

261 After excluding highly correlated variables, we retained 18 traits or  
262 trait states for further analyses. Individual correlations between the  
263 DDi and each functional trait are shown in Tab. 2.

264 The DDi was found to be significantly correlated with the  
265 following variables: four of the larval feeding modes  
266 (phytophagous on bulbs, saproxylic, phytophagous on roots, and  
267 zoophagous), body length, flight ability, distribution, body pile,  
268 body shape, inundation tolerance and duration of larval  
269 development. The most significant correlations occurred between  
270 DDi and traits related to specific larval food types such as  
271 phytophagous on bulbs, saproxylic, phytophagous on roots and  
272 zoophagous. In contrast, there does not appear to be a significant

273 correlation between DDi and the saprophagous larval feeding  
274 mode.

275

276 Table 2. Correlations between the dark diversity index (DDi) and  
277 functional traits.

278

279 Three larval feeding modes were the most significant variables  
280 according to %IncMSE values (saproxyllic = 54.2, phytophagous  
281 on bulbs = 53.2, phytophagous on roots = 51.9) (Fig. 4), matching  
282 the three most significant individual correlations with the DDi  
283 (Tab. 2). Flight period, inundation tolerance, body shape and  
284 human impact tolerance were also found to be very important  
285 explanatory variables contributing to the probability of a species  
286 being part of dark diversity, each of which presented a %IncMSE  
287 value > 40.0. However, when assessed individually, human impact  
288 tolerance and flight period were no longer important explanatory  
289 variables.

290

291 Figure 4. Functional traits and trait states showing relative  
292 importance (%IncMSE) for dark diversity of hoverflies in  
293 Southeast Europe.

294

295 **Discussion**

296 Several studies in recent years have addressed the significance and  
297 possible applications of investigating dark diversity (e.g. Pärtel *et*  
298 *al.*, 2011; 2014; Ronk, 2016; Lewis *et al.*, 2017). However, to the  
299 best of our knowledge, no previous study has addressed the dark  
300 diversity of any insect group, which is perhaps unsurprising given  
301 that invertebrates are usually neglected in conservation studies  
302 (Zamin *et al.*, 2010; Cardoso *et al.*, 2011). Thus, our study  
303 represents the first extensive assessment of dark diversity among  
304 hoverflies across SE Europe. Furthermore, it reveals which  
305 functional traits of hoverflies can be linked to dark diversity,  
306 potentially revealing why certain species are often missing from  
307 habitat types in which they could potentially thrive.

308

### 309 **Levels of hoverfly dark diversity across vegetation types**

310 Southwest Balkan sub-Mediterranean mixed oak forests showed  
311 the highest level of dark diversity and lowest level of observed  
312 diversity. This outcome may be because oak forests are in decline  
313 generally all across Europe and most of the respective habitat  
314 patches are small and scattered, limiting their carrying capacity and  
315 inhibiting the metapopulation dynamics important for sustaining  
316 populations. Southwest Balkan sub-Mediterranean mixed oak  
317 forests have been exposed to intense anthropogenic pressure over  
318 the last 2000 years, subjected to constant felling (Mansourian *et*

319 *al.*, 2013). This pressure has resulted in overt destruction, size  
320 reductions and fragmentation of these forests, as well as promoting  
321 edge effects (Robinson *et al.*, 1995). Jovičić *et al.* (2017)  
322 investigated the effect of landscape structure on the two largest  
323 hoverfly genera (*Merodon* Meigen, 1803 and *Cheilosia* Maigen,  
324 1822) and suggested that habitat connectivity influences the  
325 species composition of habitats. Moreover, it has been  
326 demonstrated that edge effects also impact physical characteristics  
327 of the environment, leading to increased temperatures and reduced  
328 humidity (Murcia *et al.*, 1995). Additional causes of these declines  
329 are pathogenic infection of oak species (Jung *et al.*, 2010) and  
330 extreme weather (drought or frost) (Thomas, 2008). However, it is  
331 human impact that appears to be playing a crucial role in  
332 maintaining deciduous oakwood forests. For instance, occasional  
333 fires have been shown to promote the occurrence of oak (Abrams,  
334 1992), and it seems that the recent decline in applying traditional  
335 management strategies (such as burning) has negatively affected  
336 oakwood assemblages (Hedl *et al.*, 2010). A second vegetation  
337 class that presented high levels of dark diversity was Alpine,  
338 subalpine and oro-Mediterranean. Multiple studies have  
339 demonstrated the sensitivity of these habitats (Ruiz *et al.*, 2008;  
340 Gillaredeli *et al.*, 2013). The main reasons for the vulnerability of  
341 this vegetation type are increased human impact through



342    infrastructural development (Pintaldi *et al.*, 2017) and high levels  
343    of grazing (Firm *et al.*, 2009). Moreover, patches of alpine and  
344    subalpine habitats are usually small and fragmented. Thus,  
345    multiple characteristics of the Alpine, subalpine and oro-  
346    Mediterranean vegetation class could be responsible for the high  
347    dark diversity of hoverflies we report for this class.

348    Mediterranean mixed forests showed the lowest level of dark  
349    diversity. Although Mediterranean habitats have been reported as  
350    seriously degraded due to intensive human actions (King, 1997;  
351    Blondel, 2006), it would seem that they are resilient to existing  
352    pressures, at least in terms of their capability of hosting a large  
353    proportion of hoverfly species. Many reports (di Castri, 1981;  
354    Thompson, 2005) have explained this phenomenon as resulting  
355    from long-term adaptation of ecosystems to humans in this region,  
356    even going so far as to apply the term “co-evolution”. Large  
357    expanses of this vegetation type, which are highly connected,  
358    enable the existence of many species, including those that require  
359    large areas to maintain viable populations, resulting in only 33  
360    species being identified as contributing to dark diversity. Beech  
361    and mixed beech forests showed the second lowest level of dark  
362    diversity, and presented the largest species pool and greatest  
363    observed diversity. This outcome can be explained by the fact that  
364    these forests are among the best preserved in SE Europe (Meyer *et*

365 *al.*, 2003), providing suitable microhabitats for both larvae and  
366 adults of hoverflies. Additionally, this result may be partially  
367 attributable to geographical proximity to degraded oak forests from  
368 which hoverflies may have migrated to find more favorable  
369 conditions.

370

### 371 **Functional traits contributing to dark diversity**

372 Three different larval feeding modes were identified as the most  
373 significant traits contributing to dark diversity. The importance of  
374 larval type and particularly their food preferences has been well  
375 established for many other aspects of hoverfly biology and ecology  
376 (Schweiger *et al.*, 2007; Haenke *et al.*, 2009), and our results  
377 suggest that these factors dictate which species might survive in  
378 habitats that are apparently adequate. Larval feeding mode  
379 indirectly reflects the level of specialization of a species.  
380 Saproxylic hoverfly larvae, as well as phytophagous species that  
381 develop in bulbs and roots, are considered specialists (van Veen,  
382 2004, Müller *et al.*, 2011). Generalist species are widely regarded  
383 as being at an advantage compared to specialists in adapting to  
384 changing environmental conditions (Biesmeijer *et al.*, 2006,  
385 Barthel *et al.*, 2014). Generalist species are likely favored under  
386 conditions of detrimental change and should constitute the majority  
387 of observed diversity, whereas specialists may be absent from

388 impacted habitats and contribute towards dark diversity. Different  
389 saproxylic hoverflies require different stages of wood decay for the  
390 development and nutrition of their larvae (Speight, 1989), which is  
391 particularly important in clear-cut forests without tree retention  
392 where the microhabitats of these species are directly destroyed  
393 (Larrieu *et al.*, 2012). Due to their high level of specialization,  
394 saproxylic hoverflies have no alternative for their development.  
395 However, changes in forest management (heterogeneity of trees in  
396 terms of age and size structure) may increase saproxylic hoverfly  
397 diversity (Remeer, 2005). Regarding phytophagous larvae (both  
398 those developing in bulbs and in roots), their specialization is  
399 reflected in the connection to a specific plant species. Thus,  
400 geographical distributions of phytophagous species are limited by  
401 the existence of suitable habitat for their host plants, which is  
402 particularly important when species are monophagous (Müller *et*  
403 *al.*, 2011).

404 With further regard to host dependency, the period during which  
405 species fly was also revealed to be of high importance for dark  
406 diversity in our RF analysis, but not when tested individually.  
407 Flight period of hoverflies is directly linked to food resource  
408 availability, with a temporal mismatch between hoverfly activity  
409 and when host plants representing their primary food source  
410 flower. Increasing temperatures caused by climate change might

411 lead to further phenological asynchrony (Memmott *et al.*, 2007),  
412 which would have a serious negative impact on specialist species.  
413 Moreover, exploitation of food resources is dependent on other  
414 functional traits. Thus, complex interactions between flight period  
415 and other traits are likely to have a synergistic effect on dark  
416 diversity.

417 Our results also indicate the significance of inundation tolerance  
418 for the dark diversity of hoverflies. It is reasonable to assume that  
419 species with lower inundation tolerance contribute more to  
420 hoverfly dark diversity. Inundation-tolerant species can adapt to  
421 wet habitats and achieve higher species richness under those  
422 environmental conditions (Keil *et al.*, 2008), reflected in their  
423 higher levels of observed diversity. Additionally, inundation  
424 tolerance likely plays a crucial role in the ability of species to  
425 survive challenging conditions. For example, dark diversity of  
426 hoverflies is lowest in Mediterranean mixed forests, even though  
427 flooding and extensive land degradation and erosion often occur in  
428 that habitat (Poesen & Hooke, 1997).

429 Body shape is significant in shaping patterns of dark diversity  
430 because it influences species' dispersal ability, with species  
431 contributing to dark diversity in general having lower dispersal  
432 capacities (Riibak *et al.*, 2015). Even though other measures  
433 directly related to dispersal ability were not identified as being of

434 high importance to dark diversity in our study, body shape still  
435 provides useful insights into the potential of a species to disperse.  
436 This functional trait contributes to species being able to overcome  
437 challenging environmental conditions, as well as to extend their  
438 current range and invade new suitable areas. Additionally, species  
439 with well-developed dispersal abilities are less affected by habitat  
440 fragmentation, as they can migrate between suitable habitat  
441 patches (Thomas, 2000). Apart from its link to dispersal ability,  
442 body shape might also contribute a hitherto unknown mechanism  
443 of physiological or behavioral adaptation important for dark  
444 diversity for which we currently have no evidence.

445 Tolerance of human impacts determines the ability of a species to  
446 persist in increasingly changing environments where agricultural  
447 intensification, intensive grazing, forestry or urbanization are  
448 taking place, ensuring resilient species have an advantage over  
449 more sensitive ones (Winfrey *et al.*, 2011). Evolutionary processes  
450 through which resilience develops not only result in species  
451 surviving and reproducing in impacted habitats (Souza *et al.*,  
452 2014), but also endow robustness against other types of  
453 disturbances (Basley *et al.*, 2018). Accordingly, widely distributed  
454 generalist species with the ability to thrive in different types of  
455 habitats are those most likely to be resilient to human impacts  
456 (Schweiger *et al.*, 2007).

457

458 **Application of dark diversity concept in hoverfly conservation**

459 Investigation of dark diversity can contribute to prioritization of  
460 conservation efforts of both species and their habitats. Despite this,  
461 a small number of research studies has tackled this topic (Yoshioka  
462 *et al.*, 2014; Ronk *et al.*, 2015, Lewis *et al.*, 2017, Moeslund *et al.*,  
463 2017). These studies highlight two main reasons for studying dark  
464 diversity in the light of conservation. Firstly, high levels of dark  
465 diversity in certain areas could imply the existence of  
466 environmental disruptors. Secondly, apparently suitable areas that  
467 exhibit a large portion of missing species have great restorative  
468 potential. Thus, assessing dark diversity in these regions could  
469 inform to what extent we can expect conservation activities to be  
470 prosperous. Bearing this in mind, our results indicate that hoverfly  
471 habitats within Southwest Balkan sub-Mediterranean mixed oak  
472 forests and Alpine, subalpine and oro-Mediterranean vegetation  
473 should be targeted for conservation.

474 Beside contribution to the conservation of habitats, dark diversity  
475 studies enable more precise conservation prioritization in respect  
476 of species-based approach. Namely, linking functional traits and  
477 dark diversity may guide conservation efforts towards more  
478 sensitive species. Our study shows that certain traits such as highly  
479 specialized larval feeding modes, lack of inundation tolerance or

480 flight period promote dark diversity of hoverflies. Identifying  
481 species possessing these traits could be an additional criterion  
482 when deciding which species should receive conservation  
483 attention.

484

#### 485 **Conclusion**

486 Overall, our study shows that hoverfly dark diversity to varying  
487 degrees occurs in every vegetation type in SE Europe. We found  
488 larval feeding mode to be the trait of greatest importance to  
489 determining species potential to be a part of dark diversity.  
490 Establishing which functional traits are responsible for dark  
491 diversity can help identify the processes causing species to be  
492 absent from their species pool in a given habitat. Additionally,  
493 these results contribute to more precise conservation prioritization  
494 of both hoverfly species and their habitats.

495

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507 design of the study, MM, SP and PC wrote the paper; AV, MM, SP  
508 and BI participated in data collecting; MM, SP and PC performed  
509 the analyses, MM, SP and BI prepared the figures; all authors  
510 contributed to manuscript with comments and revision.

511

512 **Conflict of interest disclosure:** We certify that we have no actual  
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514

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- 836

837 **Table legends**

838 Table 1. Functional traits and trait states of hoverflies in SE

839 Europe.

840

841 Table 2. Correlations between the dark diversity index (DDi) and

842 functional traits; rs, Spearman's rank correlation coefficient; H,

843 Kruskal-Wallis statistic.\*  $p < 0.05$ , \*\* $p < 0.01$ , \*\*\* $p < 0.001$ .

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862 **Figure legends**

863 Figure 1. Schematic diagram illustrating species pool, observed  
864 and dark diversity.

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866 Figure 2. Vegetation classes in Southeast Europe. A-Alpine,  
867 subalpine and oro-Mediterranean vegetation, B-Montane spruce  
868 and mixed spruce forests, C-Montane pine forests, D-Acidophilous  
869 oak and mixed oak - hornbeam forests, E-Beech and mixed beech  
870 forests, F-Thermophilous mixed bitter, pedunculate or sessile oak  
871 forests, G-Southeast Balkan sub-Mediterranean mixed oak forests,  
872 H-Southwest Balkan sub-Mediterranean mixed oak forests, I-  
873 Pannonian lowland mixed oak forests and steppes, J-Mediterranean  
874 mixed forests, K-Hardwood alluvial forests, wet lowland forests  
875 and swamps.

876

877 Figure 3. Number of species in dark diversity (pale purple),  
878 observed diversity (mid purple) and in the species pool (dark  
879 purple) for each vegetation class (A-K, see Fig. 1 legend).

880

881 Figure 4. Functional traits and trait states showing relative  
882 importance (%IncMSE) for dark diversity of hoverflies in  
883 Southeast Europe.

884